

the fruits may allow for wind dispersal. Seeds of *S. trifolia* have been germinated after scarification and freezing (Dore, 1962).

None of the species of *Staphylea* has any reported economic use other than as a garden ornamental. It has often been suggested that these shrubs should be more widely planted because of their pleasing flowers, interesting fruits, and shade tolerance.

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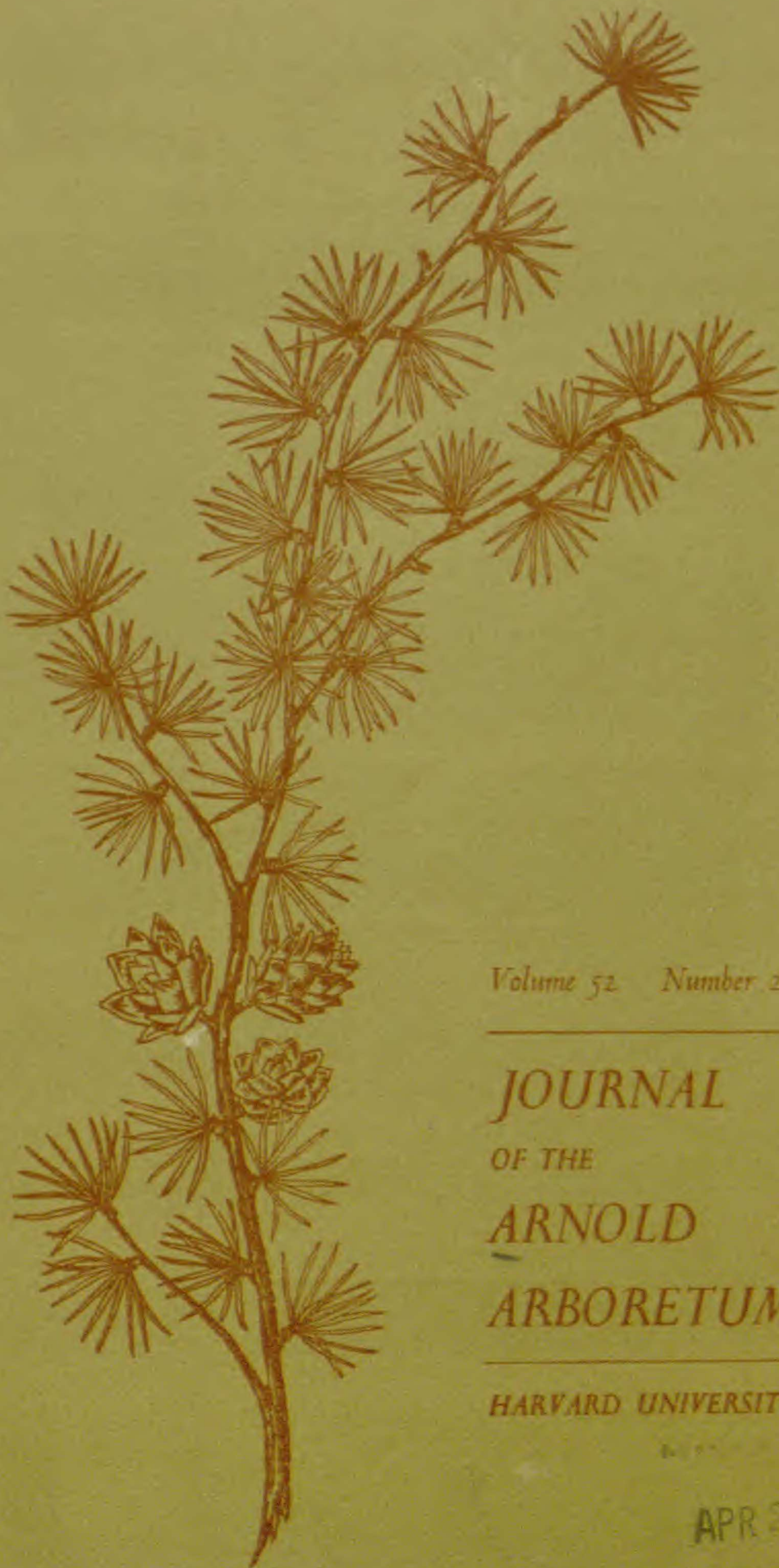
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52 p 73



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WHAT IS THE PRIMITIVE FLORAL STRUCTURE
OF ARALIACEAE?

RICHARD H. EYDE AND CHARLES C. TSENG

"THE GENERA OF Araliaceae that are most remote from Umbelliferae are *Plerandra*, *Tetraplasandra*, and their near relatives; in general, these are the genera that are distinguished by a greater number of stamens or carpels. In an arrangement where the Umbelliferae follow the Araliaceae, one would have to place these genera at the beginning of the family. Since we can observe within the Araliaceae a very gradual transition from species with many stamens and carpels to those characterized by 5 stamens and 2 carpels, it is not improbable that we have here a reduction series and that the forms placed at the beginning of the generic sequence also represent the oldest types of the family." (Harms, 1894, p. 21, 22.)

"A few of the Araliaceae have ten or more petals, stamens, and carpels in a regular, symmetrical arrangement. These polymerous types have sometimes been regarded as primitive within the family, but they more probably have undergone a secondary increase in the number of parts of each kind. Pentamerous flowers are here regarded as primitive in the family and order." (Cronquist, 1968, p. 278.)

The first quotation, translated rather freely from Harms's monograph of the Araliaceae, cautiously expresses a view that has long prevailed concerning floral evolution in the family. H.-L. Li, in his revision of the Chinese Araliaceae, put it more emphatically. Of *Tupidanthus*, he wrote: "Its primitiveness . . . as indicated by the numerous stamens, ovary-cells, and styles, is unquestionable." Baumann-Bodenheim (1955), a leading student of fruit structure in Araliaceae and Umbelliferae, recognized a five-stage reduction series from the many-carpellate ovary to the pseudo-monomerous ovary. As far as we know, Cronquist is the first author to question the "unquestionable" primitiveness of the polymerous flower in this alliance.

Ordinarily, primitive floral characters might be sought in genera with primitive wood characters; experience shows such an association of characters occurs fairly often. However no wood anatomist has yet carried out a thorough investigation of the Araliaceae, and the limited data available suggest no simple relationship between floral characters and xylem

characters. The most detailed observations to date (Rodriguez, 1957) show advanced xylem characters in temperate herbs (*Aralia californica*, *A. hispida*) and in the vine *Hedera helix*, where one would expect to find specialization, but primitive xylem characters such as scalariform perforation plates and heterogeneous rays are distributed among genera that differ greatly with respect to numbers of floral parts. Of course, future work on the wood anatomy of Araliaceae may reveal correlations with floral structure that are not now apparent. It should be kept in mind, however, that at least some of the Araliaceae have evolved through repeated radiation on oceanic islands, radiation apparently accompanied by complex changes in growth habit (e.g., trees to shrubs and back to trees again; see Carlquist, 1965, p. 191). If such changes were sufficiently widespread, the usual trends of wood evolution might be difficult or impossible to find in this family.

Since associated xylem characters are not presently of value for assessing the evolutionary status of polymeric flowers, we looked for an association between vascular characters—more specifically, vascular characters of the gynoecium—and the number of floral parts. One basic tenet of evolutionary plant morphology is that flowers with sepals, petals, stamens, and carpels united in various ways have evolved from flowers with all appendages free. Similarly, a flower in which all of the principal vascular bundles are separate is more primitive than one in which the principal bundles are variously united. In a group with inferior ovaries, the degree of union between dorsal carpel bundles and peripheral bundles (supplying epigynous appendages) may differ in different taxa, thus providing an indication of evolutionary advancement (Eames & MacDaniels, 1947, *Figure 167*; Eyde, 1967, *Figures 5–8*). Baumann (1946) found that the Araliaceae differ among themselves in this regard,¹ but his observations were not detailed enough for our purpose; so we surveyed the family to establish the taxonomic distribution of the differences. Simultaneously, and for like reasons, we examined our material for differences in the position and the degree of union of ventral bundles.

MATERIAL, METHOD

TABLE 1 lists the collections from which our observations are taken, together with the manner of preparation. Whenever possible, we used fluid-preserved specimens, usually flowers, occasionally fruits. Some we collected ourselves; others were obtained from helpful colleagues (see acknowledgments); for the most part, however, we had to make do with herbarium material, as indicated in the table. Herbarium specimens of most Araliaceae carry a great many flowers or fruits; so a few can usually be taken for anatomical study without detriment to the collection. In most cases, we removed two to four flowers for serial sectioning and

¹ Baumann (later known as Baumann-Bodenheim) had his own manner of describing the derived form of the gynoecial vascular system. Where we say the dorsal carpel bundles are united with peripherals, he would say the carpel bundles are absent (Baumann, 1946, p. 63 and *Table 1*).

a similar number for clearing; however, we occasionally made our observations from a single flower, found nothing of much interest, and declined to remove others from the sheet.

We sectioned the flowers transversely, supplementing with longitudinal sections only in the case of *Tetraplasandra* (on which we have written a separate paper; Eyde & Tseng, 1969). We cleared whole flowers by treating them with NaOH and chloral hydrate, then passed them through an ethanol series into toluene for examination. If this treatment did not reveal the vascular system in sufficient detail, we next transferred the cleared flowers from toluene to melted paraffin, cast the paraffin into blocks, and cut the blocks into pieces with a razor blade, using a dissecting microscope to orient the smaller specimens. When we subsequently dissolved away the paraffin matrix with toluene, the cut pieces often showed vascular detail not visible in whole cleared flowers.

OBSERVATIONS

TABLES 2 and 3 summarize the important features of gynoecial vasculature for each of the examined species; the tables also list the number of petals, stamens, and carpels for each. Sepals are not listed because the calyx is often poorly developed or lacking in Araliaceae. In TABLE 2, species are arranged in four groups, according to whether their flowers are best described as polymerous, 5-merous in all whorls, 5-merous with 2-merous gynoecium, or 5-merous with 1-locular gynoecium. Assignment is rather arbitrary in some cases, but most species fall readily into one or another of these groups. Literature citations accompany a few of the entries; in such cases, the vascular characters are not our own observations but are taken from an illustration or from descriptive comments in the cited work. *Tetraplasandra* species vary so greatly with respect to meristic characters that we decided to list them separately (TABLE 3).

In many species of Araliaceae — especially those with polymerous flowers — the number of floral appendages in each whorl varies from flower to flower. Obviously, we could not expect to establish the limits of variation for such species by examining only a few flowers of each (moreover, some of the flowers had petals or stamens missing); therefore, the counts given in TABLE 2 rely heavily on published descriptions. Several of our entries for petals and stamens of *Oreopanax* species are based on Smith's (1941) generic description in *North American Flora*, in which flowers are said to be "5 (rarely 4- or 6)-merous." In general, Smith's treatment does not give the numbers of floral parts for individual species. We use quotation marks wherever we have made no count of our own. For the most part, however, we did make one or more counts which fell within the limits given in the literature; in such cases we list the literature limits without quotation marks. When our count deviated from the counts of other authors, we usually expanded the literature limits to accommodate our observation. For instance, Clarke's treatment of *Schefflera* (*Heptapleurum*) *hasiana* in Hooker's *Flora of British India* (see generic de-